PROCEEDINGS

OF THE

CALIFORNIA ACADEMY OF SCIENCES

Fourth Series

Vol. XXV, No. 7, pp. 215–220 June 1, 1944

ALICE EASTWOOD
SEMI-CENTENNIAL PUBLICATIONS

No. 7

WATER AND PLANT ANATOMY

BY

GEORGE J. PEIRCE
Professor of Botany, Emeritus
Stanford University, California

Fortunately the processes of Nature go on whether man understands them or not; but curiosity, which has led man to enquire about everything inside and outside himself, has brought not only the satisfaction sought, but has stimulated continued enquiry, has led to the development of powers formerly unsuspected, and to the recognition of reasons why the powers are not unlimited. It has been discovered that living things require air to breathe, water to absorb, food to take in; what it is in air, water, food which is indispensable and not merely stimulating; and some of the relations between the worlds outside and inside the living thing. One of these relations concerns itself with the intake and outgo of one or other of these things—air, water, food. In this paper in honor of an associate of many years I wish to consider one of these relationships, thereby contributing also to an understanding, or at least a conjecture, as to why grass, chaparral, or forest should be the natural cover of respective areas.

The body of the higher land plants consists of tissues among which the various functions are divided and by which the various needs are met; but, while there is division of labor, each tissue and each organ of the plant may perform secondary functions, or be the seat of subsidiary phenomena. Thus the green leaf, primarily for the production of food, is the seat of maximum gas exchange and of water loss. The green leaf represents in its shape, size, distribution, anatomy, duration, and even number, the adjustment which each individual leaf, as well as the whole plant, makes among these, and many other, less evident, phenomena. Similarly the root, primarily for the mechanical support of the plant and the intake of water, must provide also for passing the water on to other parts of the body. But obviously these tasks vary according to diverse or changing external conditions, the intake of water from moist soil in the rainy season appearing to be easier and more understandable than by the same root from the same soil in the dry season. The facile statements that water intake by roots is an osmotic phenomenon, or that "work is done," ignore the fact that, under conditions very different from those of well-watered Europe, the relative densities of the solutions in root and in soil are also very different.

In order to provide the path of water movement from soil to air through the body of the plant there must be a vascular system, again so flexible that it will meet the need of the plant in all of its circumstances, ranging from saturated soil and air to soil and air almost dry. Combining mechanical support and water lift, one finds the vascular tissues variously strengthened and the vascular tissues themselves variously composed of elements as different as the small-one-celled tracheids of the wood of the conifers and the large many-celled vessels of the annual herbaceous plants of the rainy season. Furthermore, the same individual plant may regularly produce different conducting tissue in the same year according to the external environment.

I should like now to cite some of the evidence on which these statements rest, specifically in regard to the conducting tissues of the vascular land plants.

As shown in previous papers,[1] the quantity and the physical state of water in the conducting tissues of plants, and their parts, varies from a liquid exerting outward pressure to a vapor under internal tension or suction: from columns of liquid water more or less completely filling the lumina of ducts and tracheids to sheets of liquid water on and in the material of the walls of ducts and tracheids, and enclosing masses of water vapor filling the lumina of the vascular elements. We are familiar with the phenomena of bleeding, which are the evidence of internal pressure, and only less familiar with the phenomena of transpiration or evaporation, which result in tension (traction) within the water mass in the plant body. At seasonal or other intervals the water in the vascular system of the land plant undergoes these complete changes, from liquid to vapor, from pressure to tension ("negative pressure"). Perennial land plants must survive these changes or succumb, either locally or extensively. Many annual plants cannot maintain themselves when the procession of the seasons from wet to dry entails these changes in the quantity and the state of the water within their conducting systems. Examination reveals that their vascular anatomy does not meet the requirements of adequate water holding and water lifting.

Between the so-called "water reservoirs,"[2] which are cells and tissues evidently enlarged and otherwise fitted for containing water in their vacuoles,

[1] Peirce, G. J. The state of water in ducts and tracheids. Plant Physiology, 11, 1936, and literature there cited.

[2] See Haberlandt, G. Physiologische Pflanzenanatomie, p. 371 *et seq.* 6th ed. 1924 or later, on water storage and water storing tissues.

and the wet walls which not merely contain but actually *hold* water with great tenacity, there are many intermediates, differing from one another as do the environments in which the plants live. These wet walls vary in thickness as they do in hardness and stiffness. They may look as if they were mechanically strong where little or no mechanical strain can develop; but they may show by their chemical composition that they fix—adsorb and incorporate—water, perhaps in the manner in which the water of crystallization is incorporated in blue copper sulphate. It is recognized that the crystalline form and the crystalline state of copper sulphate depend upon the two constituents of the crystals, water and copper sulphate. Similarly, but to a certain point only, and also only partially, the shape, and the thickness, of cell walls depend both on the chemical composition (cellulose derivatives and their accompaniments) of the cell wall and water. Collenchyma tissues, which are mechanically weak though looking as if they might have tensile or compressive resistance, do store amounts of water which are large in proportion to the mass. The amount of heat required to drive off all of this water indicates the force with which this water is bound: and the shrinkage shows no less plainly how much the form depends upon the constituent water.

Turning now to specific instances as illustrating these general statements, one may consider *Montia perfoliata* (Donn) Howell, "Miner's lettuce," a succulent, low, annual herb which begins soon after the first rains have considerably wet the soil of natural and cultivated areas, and which expires while the moisture content of the air and of the soil is still high. The appearance of the root system suggests that it is adequate as an absorbing organ; the area and composition of the leaves and their surface are such that transpiration (evaporation) into warm, dry air, while considerable, need not be excessive, provided the means of moving water, even through the limited distance of the height of these small plants, be adequate. But examination of cross and longitudinal sections of the stem discloses conducting tissues in vascular bundles too few and too small to meet the need. Furthermore, the wood (xylem) of the vascular bundles consists of ducts (vessels) of relatively large size and thin walls, and comparatively few and thin-walled tracheids. These plants are mechanically weak, but they successfully carry their own weight and the increasing load of seeds and fruit, breaking only when unusual force is applied. The supporting tissues of Miner's lettuce are sufficient to keep it erect: but when the strain of drying air and soil is put upon the conducting tissues, they are unequal to the need of moving water rapidly from the roots which take it in to the leaves which lose it. The composition of the vascular bundles is diversified and interesting, but they are inadequate and the plants die.

If one turn to other native herbaceous plants, the "tar weeds" (*Hemizonia sp?*), one finds much longer lived annuals which start from seed at about the same time as *Montia* but which persist throughout the dry season till the rains come again. The plants form more or less perfect rosettes of largish rather fleshy leaves quite close to the ground. These are the food-manufacturing organs which are active for a long time and which lose water comparatively slowly because of their position close to the ground, their hairy covering, their water-proofing by cell-walls and secretions. The stalks which bear the flowers from early summer till late fall are slender, dry, woody, and their leaves are small and narrow. The surface of stalks and leaves is waterproofed. The structure is compact, as one would expect in a plant of such xerophytic habit, with adequate mechanical support. The vascular bundles are composed of a strikingly large proportion of thick-walled tracheids, with few and small ducts. The limited area of the surface of the flowering stalks and the composition of their vascular bundles insures a sufficient water transport to offset the water loss into the dry air.

If one compare these two annuals with a plant which has a perennial underground root, namely *Echinocystis fabacea* Naud., common manroot, one sees long, slender stems which climb by means of branched tendrils very sensitive to contact. The leaves are large and thin, smooth or only sparsely spiny, not thoroughly waterproofed nor structurally provided with water-holding materials. The stems are mechanically weak, except that their tensile strength is considerable, especially when dry: but their vascular bundles have long been the admiration of the plant anatomist because of the arrangement and the strikingly large size of the ducts and sieve-tubes. Tracheids make up only a small part of the wood. In the underground roots which, in older plants, may attain the size of a half barrel, or even larger, there is a great store of water; but in spite of the spectacular vascular anatomy, the leaves and stem dry and die very soon after the onset of the dry season. Furthermore, the length to which the leafy stems will grow seems to be directly related to the humidity, as well as the temperature, of the air—the higher the humidity during the period in which air temperature makes growth possible, the longer the stems become. In "wet springs" when, because of occasional rains on thoroughly watered ground, air as well as surface soil remain damp, the stems may attain surprising lengths (30 feet) as they climb over fences, bushes, and grass. On the other hand, the same underground roots give rise to decidedly shorter stems in the "dry springs," when rains are infrequent or do not occur at all.

One sees the same thing in the common garden sweet pea which, under various conditions of soil and air temperature, moisture, etc., produces slender stems of very different lengths from seeds of the same variety. Assuming the same treatment otherwise of soil and water, one's sweet pea vines will grow tall or remain shorter, they will continue to grow in length or they will stop, according to the need of carrying water in quantity and at speed through the stems from roots to leaves. Where air dryness makes transpiration from the leaves too rapid for the vascular bundles of the stems to offset, no matter how scrupulously the bed may be ground-watered, the stems promptly cease to elongate. The water-carrying capacity of the stems, the size and composition of the vascular bundles, seem to determine the height of the plants.

In all of the plants thus cited, as well as in all the rest, the anatomical structure of the stems may be considered to be hereditary; but while the plants may vary according to circumstances, the limits of variation, as well as their behavior otherwise, seem to be set by hereditary characters, and we find the sweet pea failing to grow indefinitely in height in spite of the mechanical support of frame or trellis. The reason seems to be that the water-carrying capacity of its vascular system is limited.

Aesculus californica (Spach) Nutt., the buckeye, or horse chestnut, is a small, spreading tree which puts forth its light green leaves, and loses them, the earliest of our native perennials. Its leaves are large and thin; one might call them delicate, but their skeleton is strong enough to carry a very considerable expanse. They fall apparently in accordance with the amount of water available in the soil, those buckeye trees becoming bare earliest which are rooted in dryest or thinnest soil, and those retaining their leaves longest are rooted where more water is available. However, this is not necessarily the case; young buckeyes from one to five or more years old, grown in well-watered gardens, and even grown in water cultures,[3] in which there is a constantly adequate supply of water as well as mineral matters and air, lose their leaves before the cold of winter would make them fall. The reason for this behavior is to be found, I believe, in the anatomy of the wood. The xylem consists of strikingly large, relatively thin-walled ducts (vessels) with fewer tracheids or other thick-walled elements than might be expected. While the capacity to carry large volumes of water, if the water is abundantly supplied from the roots, is large, the size of the ducts and the thinness of their walls permit holding only small amounts of water. Hence the large leaves are insufficiently supplied with water as the dry season continues, and they gradually dry and fall.

If one considers now the wood anatomy, the behavior of the foliage, and some of the other traits of two native oaks, *Quercus lobata* Neé, the Valley, or White Oak, and *Q. agrifolia* Neé, the Coast Live Oak, we shall be led further. *Q. lobata* puts out its summer canopy of leaves well after the coolness of midwinter is past but with the soil water undiminished; and it retains its foliage throughout the dry season, losing the leaves apparently when soil dryness may add to the difficulty of maintaining its foliage through cooling nights, and days in which photosynthesis may lag. The Live Oak, *Q. agrifolia,* on the other hand, while also losing its leaves once a year, puts out its new crop when the days have already become warm, and at least the surface soil has begun to dry. Then the leaves of the preceding year drop off. The leaves of Live Oak are ordinarily an inch or two long, compact in form, rather thick and leathery, smooth and shiny above, hairy underneath, and well waterproofed. The leaves

[3] For six years I have maintained cultures of buckeye seedlings in one-quart milk bottles half filled with Knopp's Solution. These seedlings, one year old and older, up to six years, are bare from late August or early September till February or March in spite of the nutrient solution: and they put out new leaves in the spring at about the same time as similar seedlings outside, rooted normally in the soil. The swelling of winter buds and the putting forth of leaves were not instigated in my cultures by fresh solution: nor do I see that there is any other general cause operating on the seedlings growing wild out of doors, as well as my cultures in bottles, than the rise in temperature which is one factor in the phenomena of spring.

of White Oak are much larger, lobed, thin in proportion to their area, and not especially waterproofed. If one compare the woods of these two species of oaks one finds the xylem of White Oak containing ducts of fairly large size, whereas that of Live Oak is made up predominantly of tracheids. The wood of the latter carries enough water from the roots, even in dry soil at the end of the dry season, to keep the leaves from excessive drying, and from falling before the new crop of leaves emerges in the spring.

The wood of the conifers, as is well known, is composed mainly of tracheids which, in proportion to their diameters, have thick walls. In these thick walls much water is tenaciously held. The majority of conifers are also evergreen, retaining their leaves for two or more years. Those which are not evergreen live where there is ample moisture in soil and air. The evergreen conifers are distributed from well-watered to desert areas. Their monotonous wood anatomy enables them to meet this great range of circumstances. The vascular systems of the conifers, all built upon the same general plan, are equal to the great variety of conditions under which different species and individuals live. But the vascular systems are associated with leaves of limited area, limited water loss, and even limited number. The vascular systems can carry enough water to supply the leaves at all seasons. Only in the severest of dry seasons, in years of light winter snowfall and of rainless summers, does one see signs of suffering from lack of water. In such seasons the plants absorb what water they can from dry soil; they lose what they must from leaves restricted in area and in number—many needles fall during such summers—; they make limited growth in length and may even die back extensively. In spite of the superiority of their vascular systems, one finds the desert pines as scattered individuals, not as close stands of forest or even chaparral.

The amount of precipitation and the anatomy of the plants living in a given area are two of the factors which determine the character of the vegetation, limiting a natural area to grassland, chaparral, or forest, and correspondingly limiting what man can do in the area. Attempts to establish forest, without irrigation and other care, in regions of limited rainfall and naturally supporting only grass or even chaparral, seem unlikely to succeed because the water-carrying capacity of the wood is unequal to the need of moving water fast enough from the roots in dry soil to leaves in dry air at any but limited heights above ground. The height to which a plant can grow is the height to which its vascular system can carry water. This is determined by its wood anatomy—which is inherited—and by its environment. The relation of the anatomy to water is the dominant factor, in our environment with its long dry seasons, in the complex which is the living thing.